FUNCTION OF OLFACTORY AND VISUAL STIMULI IN POLLINATION OF *LYSICHITON AMERICANUM* (ARACEAE) BY A STAPHYLINID BEETLE

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ABSTRACT

Lysichiton americanum Hultén & St. John (Araceae) is pollinated by *Pelecomalius testaceum* Mann. (Staphylinidae), a rove beetle, which utilizes the inflorescences as a mating site and food source. The fragrance produced by the inflorescences is the first cue in the attraction of the beetles. It elicits in the beetles a search behavior for the yellow color typical of the spathe.

The pollination biology of Araceae, a family of over 2000 species, has been documented only in a few dozen cases. Many species are apparently pollinated by large scarabaeid beetles, which utilize them as food sources, mating sites, and hideouts during the day (Schrottky 1910, van der Pijl 1937, Beach 1982, Pellmyr in press). Others have trap inflorescences, where pollinators such as flies and beetles enter during the female phase of the flowers and depart after pollen has been shed on them (Knoll 1926, Vogel 1978). In a few cases, secondary adaptations to pollination by euglossine bees have been recorded (Williams and Dressler 1976, Meeuse and Morris 1984).

Most members of the family grow in tropical or subtropical regions; however, about 10 species are known from temperate parts of North America. Early in the spring, the bright yellow spathe of *Lysichiton americanum* Hultén & St. John is a prominent feature in swampy places in the Pacific Northwest. The yellow color is unusual in the family; it could be expected therefore to be of major significance in the pollination system of *L. americanum*. There are, however, no reported studies of this species. Raven et al. (1981) stated that ". . . small, actively flying [staphylinid] beetles . . ." pollinate the flowers, but did not present further evidence. In the present study, we describe the pollination system of *L. americanum*.

MATERIALS AND METHODS

Floral morphology, phenology, and pollination. Observations were made from 1 to 22 April 1984 at three localities in the Seattle area

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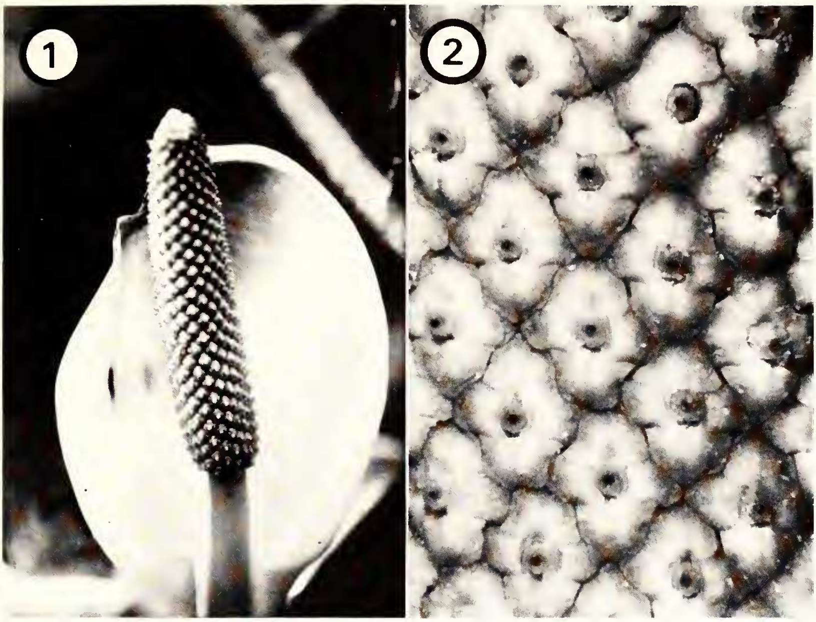
(Kirkland; Issaquah; Ravenna Park, Seattle) and near Soleduck River on the Olympic Peninsula. Population sizes ranged between 50 and ca. 500 ramets. The study included observations of floral phenology, visitor diversity, and pollinator behavior. The pollen/ovule (P/O) ratio and spectral composition of reflected light from the spathe were determined. Three ramets were put under net cages (1 mm mesh) slightly before anthesis to test for self-compatibility. Six individuals were hand-pollinated to determine whether complete fruit-set could be accomplished. In the largest population examined, three 15 × 15 cm plastic plates, covered with glycerin jelly, were put on stalks at inflorescence height to trap possible wind-carried pollen. The traps were recovered after 48 hours and checked (under a microscope) for pollen.

Flower visitors and their behavior. The identity and frequency of insect visitors was determined by observation of flowering populations for a total of ca. 30 hours. The effect of floral odor and spathe color in attraction of the primary pollinator, *Pelecomalius testaceum* Mann., was studied. A series of experiments were performed inside of a net cage (3 × 1.5 × 1 m) inside a greenhouse. Beetles were collected from inflorescences in the field in the late afternoon, starved overnight in a refrigerator at about 10°C, and released in the cage the following morning. Fifty cm from the point of release, plant parts of *Lysichiton* were presented in experiments of choice to the beetles in the following combinations: 1) two sealed petri dishes (diam. 15 cm), the first containing green leaves only, and the second a yellow spathe; 2) two sealed petri dishes, both containing green leaves but one also including a spadix concealed between the leaves and 100 small perforations in the dish, allowing passage of fragrance; 3) similar dishes as in 1, plus a visible spathe in a vase; 4) two spathes, one bearing a male-phase spadix, and the other a female-phase spadix. In each experiment 40 beetles were used, and the number of approaches and alightings to the different samples were recorded for 30 minute intervals. The glass in the petri dishes may have affected the beetles attraction to the materials kept inside because it would prevent passage of UV light; however, because reflectance off of the spathe surface was very low in the UV region, any filtering of light by the glass was deemed unimportant.

Results

Floral morphology and phenology. The inflorescence of *L. americanum* consists of an elongate spadix of small hermaphroditic flowers (Fig. 1). The 6–15 cm long spadix has 350–1350 ($\bar{x}$ = 690, s.d. 236; n = 14) flowers. Each unicarpellate flower contains one or rarely two ovules ($\bar{x}$ = 1.01; n = 163). Four stamens arise from the base of each flower (Fig. 2). Flowering within the inflorescence is syn-



FIGS. 1, 2. Photographs of *Lysichiton americanum*. FIG. 1. Inflorescence in female phase, 0.4× magnification. FIG. 2. Female-phase flowers at 4.6× magnification; the lower stamen of some flowers are ready to dehisce.

chronous or weakly acropetalous. The spadix is partly surrounded by a 15–25 cm long spathe. During the last two to four days before anthesis, xanthophyll accumulates in the spathe, which causes it to become bright yellow at maturity. When the spathe opens up, the flowers inside are in female phase. The stigmas remain receptive for 5–6 days. Two lateral stamens appear and dehisce on day five or six of stigmatic receptivity, and the two other stamens dehisce about two days later. Wilting occurs 5–8 days after start of the male phase. The inflorescence produces a distinctive fragrance from the first day of anthesis. It gradually ceases by the end of the male phase. This odor is noticeably different from the "skunk" odor of the vegetative parts.

The P/O ratio of *Lysichiton* was 76,912:1 (s.e. 2689; n = 10). Raphides were found in several pollen samples.

Breeding system experiments. Of the three inflorescences that were caged in the field and left untouched, two were recovered. Fruit-set was 100%. This suggests that *Lysichiton* is self-compatible and capable of self-pollination due to partial temporal overlap between male and female function in the inflorescences. Of the six hand-pollinated individuals, four were lost to a landfill operation, but the remaining two set 100% fruit. Conifer grains on the wind pollen traps were abundant, but no *Lysichiton* pollen was found, suggesting an absence of wind-pollination in this species.

Flower visitors. The only regular flower visitors were the beetles *Pelecomalius testaceus* (Staphylinidae) and *Plateumaris emarginata* (Donaciinae, Chrysomelidae). Individuals of a few other species of beetles and flies were found on inflorescences on single occasions, but they appeared to use them only as resting sites.

Pelecomalius testaceum was found exclusively on *L. americanum.* Individuals of this beetle species were 4–6 mm long, slender, brown and black in color, and carried considerable amounts of pollen on most body parts. They were undoubtedly efficient pollinators. Near flowering peak, about half the mature inflorescences had at least one beetle visiting when checked (Table 1). Beetles of both sexes fed on pollen—five individuals of each gender were dissected and the intestines contained pure *Lysichiton* pollen in every case. Visitors to female-phase inflorescences, which lack food reward, ran rapidly over the spadix. Slightly fewer beetles were found on pure female-phase inflorescences than on those in male phase. The inflorescences also serve as mating sites for the beetles. Males flew between inflorescences and ran over them, searching for females. When a female was found, the male always mounted her, stroked her tergites by lateral abdominal movements, and tried to copulate. Female refusal led to chases over the flowers, and if the male was too persistent the female flew to another inflorescence. When copulation occurred, the couple usually moved to a position between flowers on a part of the spadix appressed against the spathe. Covered with pollen, the beetles are hardly discerned. Alternative resting sites were in the slightly incurved apex of the spathe, or located as far as possible down the stem of the spathe. Beetles were found throughout the duration of anthesis of *L. americanum,* and beetle mating activity peaked simultaneously with flowering. One mutant genet with green fragrant spathes was never observed to be visited by *Pelecomalius.*

Individuals of *Plateumaris emarginata* were found sitting on various flower parts, often *in copula.* Their intestines were empty of pollen, and the beetles only became common by the end of the flowering season. They are poor pollen vectors because of the low rate of movement between inflorescences, combined with the small amount of pollen that adhered to their bodies. There is reason to believe, however, that *L. americanum* is its host plant, because all donaciine beetles utilize species of Nymphaeaceae or aquatic monocotyledons as larval development sites (Crowson 1981).

Experiments testing visual and olfactory stimuli on beetle attraction. The results of the experiments are shown in Table 2. In experiment one, sealed petri dishes received only occasional alightings,

TABLE 1. PERCENT ATTRACTIVE INFLORESCENCES OF *Lysichiton americanum* AT THE STUDY SITES THAT HAD AT LEAST ONE VISITING *Pelecomalius testaceum.*

Locality	n	Percent
Ravenna Park, Seattle (2 April)	86	64
(4 April)	52	42
Kirkland (16 April) (after peak)	100	15
Issaquah (16 April) (after peak)	12	25

independent of color of the content. Most beetles flew around in the cage, but almost completely ignored both dishes. When presented the green dishes in experiment two, beetle alighting frequency on the fragrant dish was significantly higher than on the non-fragrant one. Beetles typically alighted on the fragrant dish and ran over it, in some cases for about 15 minutes, looking for a place to enter. Some beetles managed to force their way into the dish, despite the fact that a green leaf was pressed tightly against the holes from the inside. When presented a fragrant, exposed spathe and the two dishes in the third experiment, visit frequency was more than two and a half times as high on the exposed spadix as it was on the green, fragrant dish ($G = 10.321$; $df = 1$; $p < 0.005$). When given a choice between inflorescences exhibiting spadices in female and male phase in experiment four, no significant preference was shown.

DISCUSSION

Our data strongly suggest that *L. americanum* is adapted for pollination by the staphylinid beetle, *Pelecomalius testaceum.* In *Arum nigrum,* staphylinids constituted a minority of all visitors, and were believed to effect some pollination (Knoll 1926). Whigham (1974) suggested that staphylinids pollinate *Uvularia perfoliata* (Liliaceae), but did not present convincing evidence. Staphylinids are common visitors in many flowers (Knuth 1898–1904, Hatch 1957), but appear to pollinate them only rarely.

The P/O ratio in *L. americanum* is about 100 times higher than for the average self-compatible species (Cruden 1977), and may be interpreted as an indication of wind-pollination. It is equally possible, however, that this ratio is the result of the function of pollen as the pollinator reward, together with the relative inefficiency of beetles as pollinators compared, for example, to bees (Pellmyr 1985). Camazine and Niklas (1984) suggested that the closely related *Symplocarpus foetidus* may be wind-pollinated, rather than insect-pollinated. This conclusion was based on the scarcity of insects, documented by the authors as well as earlier investigators (e.g., Trelease 1879), aerodynamic properties of the spathe, poor synchronization of flowering within populations (Niklas, pers. comm.),

TABLE 2. RESULTS FROM EXPERIMENTS ON FUNCTION OF COLOR AND FRAGRANCE IN ATTRACTION OF *Pelecomalius testaceum*. Numbers represent individual beetles observed during 30 minute intervals.

Experiment	No. of approaches only	No. of alightings	G-test
1.			
Spathe in sealed dish	4	1	G = 1.386
Leaf in sealed dish	0	0	df = 1; n.s.
2.			
Leaf in sealed dish	1	1	G = 14.699
Spathe hidden between leaves in perforated dish	2	15	df = 1; $p < 0.001$
3.			
Spathe in sealed dish	1	3	G = 68.002
Leaf in sealed dish	0	0	df = 2; $p < 0.001$
Spathe in vase	0	38	
4.			
Inflorescence with female-stage spadix	1	13	G = 1.202
Inflorescence with male-stage spadix	2	8	df = 1; n.s.

and considerable flexibility in flowering time between years. Although the aerodynamic properties of the open spathe of *L. americanum* are unknown, potential pollinators are present and flowering time is relatively constant between years (Meeuse, pers. comm.) and highly synchronized within populations. These characteristics together with the absence of *Lysichiton* pollen on the pollen traps suggest insect pollination rather than wind-pollination in *L. americanum.*

Successful attraction to female-phase flowers, where rewards are lacking, may be a case of "pollination by deceit" (sensu Baker 1976). The inflorescence, however, still serves the function of a mating site, a crucial resource to the beetles, and thus the system cannot be considered entirely deceptive.

The behavior experiments indicate a sequential function of stimuli in attraction of beetles. Odor alone induced search behavior, whereas non-odorous yellow dishes did not. When the entire spathe was exposed, the number of alightings increased with a factor of about 2.5. This suggests that the fragrance elicits search behavior in *P. testaceum* for yellow objects. A few similar cases are known from nocturnal as well as diurnal moths—the fragrance of *Melandrium album* (Caryophyllaceae) induces search for white objects in *Hadena* (Noctuidae) (Brantjes 1976), and several plusiine moths behave similarly when exposed to fragrance of *Platanthera* spp. (Orchidaceae)

(Nilsson 1978) and other flowers (Schremmer 1941). Although strong fragrance is typical of most beetle-pollinated flowers (Faegri and van der Pijl 1979), the sensory steps in pollinator attraction are usually not known. It is important to point out that these experiments did not allow the conclusion that the beetles possess color vision. Because we could not match green leaves and yellow spathes for brightness, it is possible that the insects only detected differences in brightness. Knoll (1926) used purple and white glass models to study the effects of odor on the pollinators of the purple-spathed *Arum nigrum.* Presence of the carrion-like odor resulted in as many visits to each of the models as to the natural flowers. The results demonstrate that the odor could attract the visitors, but his experiments are inconclusive as to whether visual stimuli are important in pollinator attraction.

Pelecomalius testaceum is apparently heavily specialized on *Lysichiton americanum* during its adult life. The inflorescence is a focal spot for mating activities, it provides some degree of shelter during mating, and it is a cornucopia of food. The life-cycle of the genus *Pelecomalius* may be closely tied to *Lysichiton.* A number of species were described by Casey (1886, 1893) from small numbers of individuals collected on or around *L. americanum* in California. Several were not recognized by Schwarz (1892), and Hatch (1957) listed only two species, both with distributions well matching that of *Lysichiton americanum.*

In Japan and the northern Pacific parts of Asia, *Lysichiton camtschatkense* grows in much the same habitats as its North American vicariant (Ohwi 1984). The only obvious difference from *L. americanum* is its bright white spathe. Studies of the pollination biology of *L. camtschatkense* could provide data for a better understanding of the evolution of interaction between *Pelecomalius* and *Lysichiton.*

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Literature Cited

Baker, H. G. 1976. "Mistake" pollination as a reproductive system with special reference to the Caricaceae. *In* J. Burley and B. T. Styles, eds., Tropical trees: variation, breeding, and conservation, p. 161–169. Academic Press, New York.

Beach, J. H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). Amer. J. Bot. 69:1074–1081.

Brantjes, N. B. M. 1976. Riddles around the pollination of *Melandrium album*

(Mill.) Garcke (Caryophyllaceae) during the oviposition by *Hadena bicruris* Hufn. (Noctuidae, Lepidoptera), I + II. Proc. Konikl. Ned. Akad. Wetensch., Ser. C, Biol. Med. Sci. 79:1–12, 127–141.

CAMAZINE, S. and K. J. NIKLAS. 1984. Aerobiology of *Symplocarpus foetidus*: interactions between the spathe and spadix. Amer. J. Bot. 71:843–850.

CASEY, T. L. 1886. Descriptive notices of North American Coleoptera. I. Bull. Calif. Acad. Sci. 2:157–264.

———. 1893. Coleopterological notices. V. Ann. New York Acad. Sci. 7:281–606.

CROWSON, R. A. 1981. The biology of the Coleoptera. Academic Press, London.

CRUDEN, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. Evolution 31:32–46.

FAEGRI, K. and L. VAN DER PIJL. 1979. The principles of pollination ecology, 3rd ed. Pergamon Press, Oxford.

HATCH, M. H. 1957. The beetles of the Pacific Northwest, part II. Univ. Washington Press, Seattle.

KNOLL, F. 1926. Insekten und Blumen. IV. Die Arum-Blütenstande und Ihre Besucher. Abh. K. K. Zool.-Bot. Ges. Wien 12:383–481 + 1 plate.

KNUTH, P. 1898–1904. Handbuch der Blütenbiologie I–III. Engelmann, Leipzig.

MEEUSE, B. and S. MORRIS. 1984. The sex life of flowers. Facts on File Publ., New York.

NILSSON, L. A. 1978. Pollination ecology and adaptation in *Platanthera chlorantha* (Orchidaceae). Bot. Not. 131:35–51.

OHWI, J. 1984. Flora of Japan, 2nd ed. Smithsonian Press, Washington, DC.

PELLMYR, O. 1985. Pollination biology of *Cimicifuga arizonica* (Ranunculaceae). Bot. Gaz. (Chicago) 146:404–412.

———. In press. *Cyclocephala*: visitor and probable pollinator of *Caladium bicolor* (Araceae). Acta Amaz.

RAVEN, P. H., H. EVERT, and H. CURTIS. 1981. The biology of plants, 3rd ed. Worth Publishers, New York.

SCHREMMER, F. 1941. Sinnesphysiologie und Blumenbesuch des Falters von *Plusia gamma* L. Zool. Jahrb. 74:375–434.

SCHROTTKY, C. 1910. Die Befruchtung von *Philodendron* und *Caladium* durch einen Kafer (*Erioscelis emarginata* Mann.). Zeitschr. Wiss. Insektenbiol. 6:67–68.

SCHWARZ, E. A. 1892. In protocol from meetings. Proc. Entomol. Soc. Wash. 2: 396.

TRELEASE, W. 1879. On the fertilization of *Symplocarpus foetidus*. Amer. Naturalist 13:580–581.

VAN DER PIJL, L. 1937. Biological and physiological observations on the inflorescence of *Amorphophallus*. Rev. Trav. Bot. Neerl. 34:157–167.

VOGEL, S. 1978. Pilzmückenblumen als Pilzmimeten. Flora 167:367–398.

WHIGHAM, D. 1974. An ecological life history study of *Uvularia perfoliata* L. Am. Midl. Naturalist 91:343–359.

WILLIAMS, N. H. and R. L. DRESSLER. 1976. Euglossine pollination of *Spathiphyllum* (Araceae). Selbyana 1:349–356.

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